STUDIES IN THE GOODENIACEAE.

I. The Life-History of Dampiera stricta (R. Br.).

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(Plates xxxvi-xxxvii and fifty-eight Text-figures.)

[Read 28th September, 1927.]

Introduction.

One of the final attainments of botanical research will be the realization of an absolute Natural System of Classification of plants.

How far this goal is from attainment is manifest, and even more apparent is the difficulty of such an achievement. The nature of the problem does not permit of its being resolved by the brilliancy of the individual. The arrangement of plants in such a manner as to show their phylogenetic relationships can be achieved only through the cumulative results of researchers throughout the ages. The magnitude of the task is colossal, but the lure of it is a splendid incentive to effort, and each worker may contribute his mite.

No phylum has received so much attention as the Angiosperms—a fact readily understood—yet, despite the efforts of systematists from the time of Linnaeus to the present day, the so-called Natural System of Classification of Angiosperms, is still largely artificial, and a matter of surmise. The Orders and even many Families are, in the main, merely aggregations of forms with similar gross characters, that is, are form groups, which may or may not consist of closely related members. The variety of Systems, which claim precedence at the present day, bears testimony to the above statement. Agreement has not even been reached as to what constitute the most primitive forms of flowering plants.

It would seem that further progress may most confidently be expected along that line of investigation which deals with the life-histories of representatives of those Families about which little or nothing beyond gross morphology is known. In this way assumptions or suspicions may be tested, and unsuspected relationships exposed.

For obvious reasons our knowledge of the life-histories of Angiosperms is largely confined to cosmopolitan forms, or to those prevailing in the Northern Hemisphere, and particularly to the Temperate Regions. It is the more desirable then to gain information regarding representatives of floras typical of the great land masses south of the Equator, such as South Africa, South America and Australasia. Most particularly does this apply to Australia, which, on account of its long isolation from adjacent continents, may well harbour forms of peculiar significance. In addition the study of endemic forms may shed light on the vexed question of the original centre of distribution of Flowering Plants.

So far, very little indeed has been done along such lines in Australia, which with a flora noted for its high percentage of endemism may supply some interesting information concerning the course of evolution.

Only two Families of plants are confined to Australia, *viz.* Brunoniaceae and Tremandraceae, but at the same time many Families find their chief expression in Australia, and beyond its borders are represented only by a few widespread species. An outstanding example of this is furnished by the Goodeniaceae, a Family which has many points of interest, but which is chiefly noteworthy on account of its indusiate stigma, and peculiar pollinating mechanism.

Such abnormalities, coupled with the puzzling distribution of the genera and species comprising the Family certainly held the attention of the writer, and suggested that an investigation of the life-history of a representative of one or more genera might not be an unprofitable undertaking.

THE GOODENIACEAE.

The Goodeniaceae comprises 12 genera which have been divided into two sections (Bentham and Hooker, 1869).

Section A. *Leschenaultia, Anthotium, Velleia, Goodenia, Calogyne, Selliera, Catosperma*—consisting of forms with two or more ovules in each loculus of the ovary, or on each side of the imperfect or rudimentary dissepiment.

Section B. *Scaevola, Diaspasis, Verreuxia, Dampiera, Brunonia*—having one or two ovules in each ovary.

Some authorities prefer to exclude *Brunonia* from the Goodeniaceae and recognize a Family—the Brunoniaceae—which is monotypic.

Engler and Prantl (1887) subdivided the Goodeniaceae into I. Goodenioideae (including all the above genera except *Brunonia*) and II. Brunonioideae with a single genus *Brunonia*.

An investigation of the life-history of *Brunonia* is obviously to be desired.

Of the twelve genera quoted nine are confined entirely to Australia (Bentham and Hooker, 1869), *viz.*:

Goodenia	.. ..	with	69 spp.
Dampiera	.. ..	,,	34 ,,
Leschenaultia	.. .. ..	,,	16 ,,
Velleia	.. ..	,,	12 ,,
Verreuxia	.. ..	,,	2 ,,
Anthotium	.. ..	,,	2 ,,
Catosperma	.. .. ..	,,	1 ,,
Diaspasis	.. ..	,,	1 ,,
Brunonia	.. ..	,,	1 ,,

while of the remaining three genera, *Scaevola* with 65 species is distributed throughout Australia, Polynesia and various other warmer sea coasts of the world. Only a few species, however, are found outside Australia.

Calogyne with three species occurs in Australia (2 spp.), and on the coasts of China (1 sp.).

Selliera with 2 species, occurs in Australia, one species being endemic, while the other extends to New Zealand and extra-tropical South America.

Willis (1919) gives a larger number of species in three of the above mentioned genera, *viz. Goodenia* 100 species, *Dampiera* 35 species and *Verreuxia* 3 species, while the Index Kewensis supplies the following: *Goodenia* 101 species, *Dampiera* 48 species, and *Verreuxia* 2 species.

Manifestly, then, Australia is the headquarters of the Goodeniaceae, since only three of the twelve genera, and these comprising only a few species, occur outside its borders.

The Goodeniaceae in conjunction with the Cucurbitaceae, Campanulaceae, Candolleaceae, Calyceraceae, and Compositae form an Order—the Campanales

(Engler and Prantl, 1889)—and it will be interesting to compare the life-history of one of the species of the Goodeniaceae with the life-histories representative of other families in the Order.

The vegetative features and general floral structure alike indicate that the Goodeniaceae are highly specialized, and relatively recent in evolution.

Genus Dampiera.

The genus *Dampiera* has been selected as the type for this investigation primarily because it is endemic to Australia, but also on account of its wide distribution throughout the Continent, and its highly specialized floral structure.

Seven of the thirty-four species occur in New South Wales. Two of these are common in the neighbourhood of Sydney, *viz. D. stricta* and *D. Brownii*, the former providing the material for this research.

Dampiera stricta is typically found growing in the bush in poor sandy soil, and in distribution ranges from the coastal districts to the dividing ranges. Reference to Plate xxxvi shows the habit to be erect, shrubby, and almost herbaceous. Normally it attains a height of from twelve to eighteen inches. The stem and leaves are of a dark green colour. The former is distinctly angular, while the alternate exstipulate leaves vary from elliptical to almost linear in shape, with the lower ones broader, toothed or entire. The leaves vary from one-half to one and a half inches in length.

The flowers which are shortly pedunculate, occur mostly in the axils of the upper leaves, but may be terminal and are either solitary or in clusters. The number and relative positions of the various floral organs are shown in Text-figs. 8-11.

The brownish gamosepalous calyx which is partially fused with the ovary is densely tomentose, and terminates in five tapering lobes. The zygomorphic corolla is blue with a yellow centre and is about three-quarters of an inch in length. This corolla is five-lobed and split deeply in the transverse plane in such a way that two almost free perianth segments occupy an adaxial position while three sympetalous segments are on the abaxial side. The infolding adjoining edges of the two adaxial segments form a pouch-like structure. All lobes are densely hairy except for the membranous margins which are glabrous.

The androecium consists of five stamens which alternate with the perianth segments, the filaments being inserted singly on the receptacle while the anthers are connate.

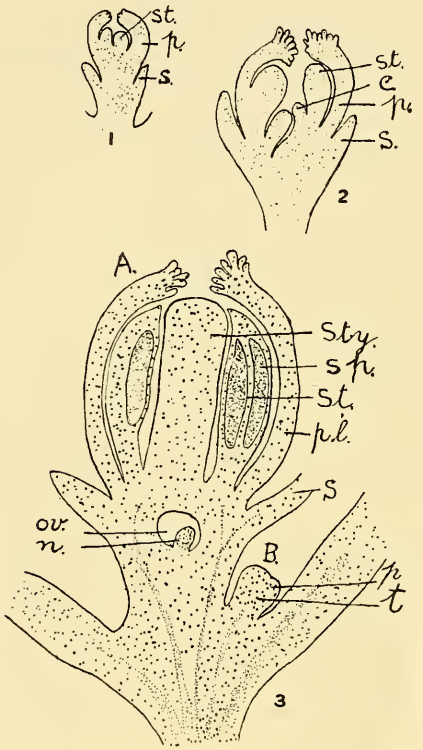
The ovary is bicarpellate, inferior, possesses one loculus, and contains a single erect anatropous ovule. When the flower is opening the style elongates rapidly, carries the terminal indusium up through the connate anthers, and curving slightly near the distal end pushes the indusium into the pouch-like receptacle formed by the auricles in the line of junction between the two adaxial segments of the corolla.

Organogeny.

The four whorls of floral organs—sepals, petals, stamens and carpels—arise in acropetal succession. The members of any one whorl alternate with the members of the whorl immediately above or below. This latter fact is shown in Text-figs. 8-11 which represent a flower bud in transverse sections. These sections are arranged in basipetal sequence.

In Text-fig. 3 at *t.* is shown the thalamus of a very young flower bud in longitudinal section. The primordia of the first or sepaline whorl are just apparent.

Text-fig. 1 shows a young bud in longitudinal section. The young sepals, petals and primordia of the stamens are easily recognizable, and are quite distinct from each other.

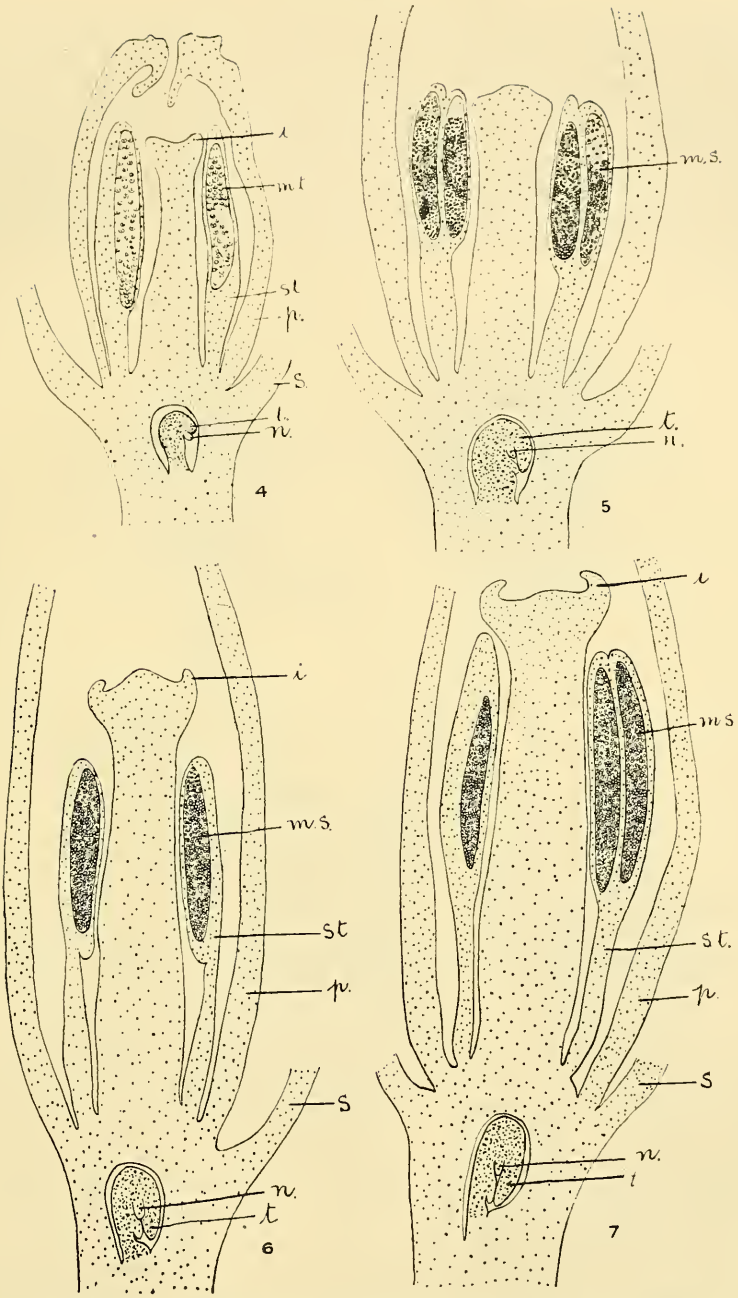


Text-fig. 1. A median longitudinal section of a very young flower bud showing young sepals, petals and stamens. *s.*, sepals; *p.*, petals; *st.*, stamen primordium. × 33.

Text-fig. 2. A median longitudinal section of a flower bud slightly older than that in Text-fig. 1. In this case the primordia of the carpels are apparent. *s.*, sepal; *p.*, petal; *st.*, stamen; *c.*, carpel. × 33.

Text-fig. 3. A median longitudinal section of a still older flower bud A, also young floral axis B. *s.*, sepal; *pl.*, petal; *st.*, stamen; *sp.*, sporogenous cells; *sty.*, style; *ov.*, cavity of ovary; *n.*, nucellus; *p.*, primordium of sepal on floral receptacle; *t.*, thalamus. × 33.

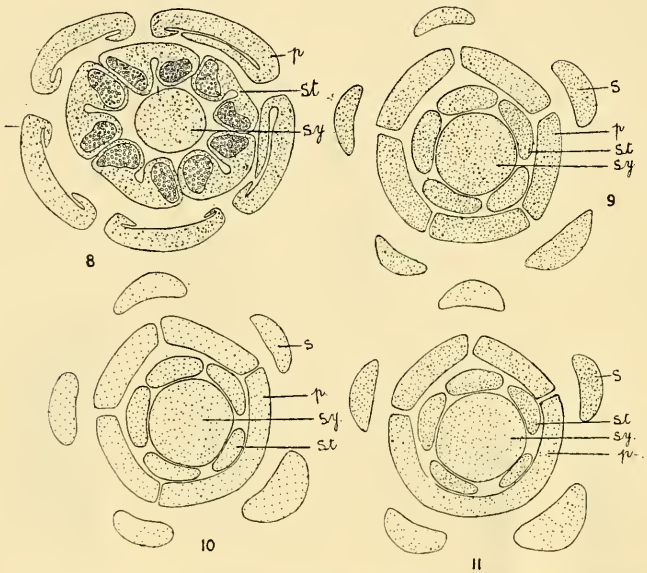
A slightly older bud shows the organs just mentioned, but in this case they have increased in size, and the primordia of the carpels are now apparent, Text-fig. 2. Even at this early stage the characteristic hairs in the distal region of the petals are apparent. Text-figs. 4-7 form a series of longitudinal sections of successively later stages in floral development. In the mature flower the sepals are fused, but the explanation supplied above indicates clearly that the primordia of these floral organs arise separately on the thalamus, and that fusion



Text-fig. 4. A median longitudinal section of a flower bud slightly older than that of Text-fig. 3. *s.*, sepal; *p.*, petal; *st.*, stamen; *m.t.*, microspore tetrads; *i.*, indusium; *n.*, nucellus; *t.*, integument. × 25.

Text-figs. 5, 6 and 7. Series of longitudinal sections of flower buds showing various stages in development. *m.s.*, microspores; interpretation of other parts as in Text-fig. 4. × 25.

is brought about later by an increase in extent of the various merismatic regions until they coalesce, and produce the gamosepalous calyx. In the case of the corolla the primordia also arise separately and continue growing independently until five distinct lobes are produced (Text-fig. 9). Later the three abaxial segments fuse (Text-figs. 10 and 11), thereby producing the lower lip of the mature structure. The two adaxial primordia, however, retain their identity until maturity is almost attained. Thus, in the fully developed flower, the corolla consists of a lower lip composed of three fused segments and an upper region, the two segments of which are distinct from the abaxial lip, and almost from each other.



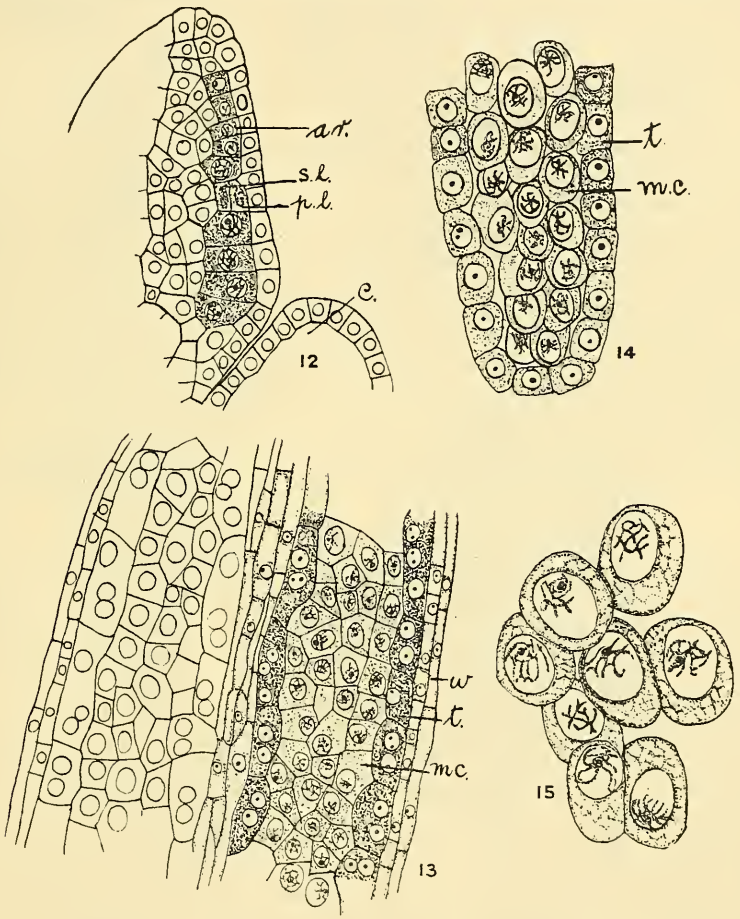
Text-figs. 8-11. Series of transverse sections in basipetal sequence of a flower bud about the same age as that shown in Text-fig. 7. The relative positions of the various parts, and their gradual fusion is illustrated. *s.*, sepal; *p.*, petal; *st.*, stamen; *sy.*, style. × 16.

The development of the androecium, however, forms a distinct contrast. In this case there is no increased merismatic activity in the region of the thalamus which gives rise to the androecium, and so the primordia of the stamens always remain distinct from each other. At a later stage the anthers increase in size with extraordinary rapidity, and the pressure set up by the impinging cells of the various stamens results in the connate condition seen in the anthers at the stage of development immediately preceding the final and very rapid elongation of the style. (Text-figs. 8 and 20).

In the young flower bud (Text-fig. 3) there is no indication of an indusium or pollen cup. As development proceeds the apex of the style becomes slightly concave (Text-figs. 4, 6 and 7), owing first of all to the relatively slow growth now taking place at the organic apex, and secondly to the increased activity of the cells around the margin of the style apex. This differential growth eventually

results in the formation of the pollen cup characteristic of the more mature flower bud (Text-fig. 53).

Again reference to Text-figs. 3-7 shows that during floral development there are from time to time most striking differences in the relative rates of growth of the style and stamens. The result of the phenomenon is that at several stages of floral development the anthers overtop the style apex, while at other intervening periods the style rises above the stamens. However, before the bud is ready to open the connate anthers overtop the apex of the style, the extremity of which



Text-fig. 12. Longitudinal section of young anther. *ar.*, archesporium; *p.l.*, primary parietal layer; *s.l.*, primary sporogenous layer cell; *c.*, young carpel. × 266.

Text-fig. 13. Longitudinal section of anther slightly older than that of Text-fig. 12. *w.*, wall of sporangium; *t.*, tapetum; *m.c.*, spore mother cells. × 266.

Text-fig. 14. Longitudinal section of anther slightly older than that in Text-fig. 13. *t.*, tapetum; *m.c.*, spore mother cells. × 266.

Text-fig. 15. Spore mother cells in synapsis. × 600.

is cup-shaped. The anthers are now mature, and the stimulus exerted by the friction of the style in passing up through the mature anthers causes the pollen sacs to split longitudinally along their inner surface and dehisce introrsely. Consequently the cup-shaped apex of the style becomes filled to overflowing with pollen grains. (Plate xxxvii, figs. 3, 4 and 5). Surely it would be hard to find a more exact or a more wonderful device in pollinating mechanisms. It may also be observed that only a very small proportion of the microspores are left behind in the pollen sacs.

Within the stamen whorl, and around the base of the style five nectaries are situated. One of these organs is shown in detail in Text-fig. 58. Such structures obviously find their role in connection with insect visitation.

A comparison between the development of the stamens and carpels in point of time shows that the procedure is normal, the former anticipating the latter stage by stage until these organs are mature. For example, the archesporial cells of the microsporangium are differentiated, while the tissue of the megasporangium is still quite homogeneous and before the integuments make their appearance (Text-figs. 3 and 12); microspore mother cells are produced before the archesporium of the nucellus is apparent (Text-figs. 13, 14, 15); pollen tetrads are segregated by the time the megaspore mother cell is distinguishable (Text-figs. 4, 26 and 27); the uninucleate microspore stage is attained, while the megaspore mother cell is dividing and giving rise to the four megaspores; dehiscence of the microsporangia and the deposition of the binucleate pollen grains in the cup-shaped indusium of the elongated style has occurred by the time the mature female gametophyte has been formed; the 8-nucleate stage of the female gametophyte is not attained until the flower bud is ready to open.

Although the microspores in the pollen cup are fully developed at this stage, they do not germinate, the stigma not yet being fully developed or receptive.

The Microsporangium—Development and Structure.

The anther consists of four microsporangia held together by connective tissue of the filament. The anthers become connate by fusion of the cuticle of contiguous cells when the stage of development—tetrad stage—shown in Text-fig. 4 is reached. The fragile nature, and the very restricted amount of tissue controlling this cohesion are illustrated in Text-fig. 20.

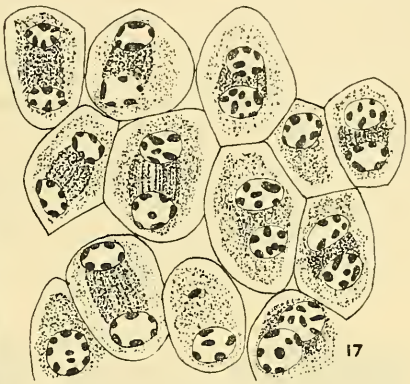
A longitudinal section through the archesporium is shown in Text-fig. 12. The archesporial cells each divide once by periclinal walls giving rise to the primary sporogenous layer (*s.l.*) and the primary parietal layer (*p.l.*). The latter divides producing the tapetum on the inside, and a wall layer one cell thick on the outside (Text-fig. 13).

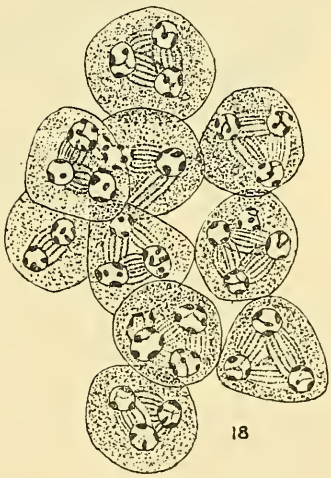
Later the inner wall layer by differential thickening becomes the fibrous layer, while the multinucleate tapetal cells become absorbed by the developing microspores. Vestiges of the tapetum are still distinguishable in Text-fig. 20.

The sporogenous cells divide twice or thrice in giving rise to the spore mother cells.

At the stage when the microspore mother cells are produced, a distinct tapetum with multinucleate cells, and dense granular cytoplasm is present (Text-fig. 13). This in turn is encased by the wall of the sporangium which on the outer side is two cells thick. Most of the spore mother cells, as shown on a higher scale of magnification in Text-fig. 15, are in the condition known as synapsis, the nuclei being relatively large, and the chromatin drawn together.

This phase is quickly followed by that indicated in Text-fig. 16, where short thick individual chromosomes can be discerned, and where various stages in reduction division are evident. These cells are found in a longitudinal section of a single microsporangium, and a series illustrating the chief phases in reduction division may be recognized on passing from one end of the section to the other. This testifies to the rapidity in development of the organ concerned. After the separation of the chromosomes, daughter nuclei are formed (Text-fig. 17). The





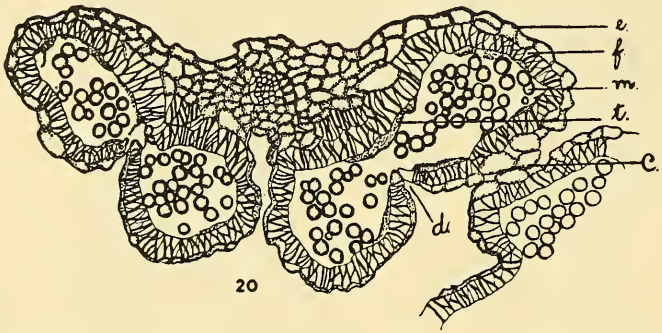
Text-fig. 16. Longitudinal section of microsporangium containing microspore mother cells with nuclei in various stages of reduction division. × 600.

Text-fig. 17. Binucleate condition resulting from reduction division in microspore mother cells. The spindle fibres are still visible in some cases. × 600.

Text-fig. 18. The four-nucleate stage preceding the formation of the microspore tetrad. The spindle fibres are still evident. × 600.

Text-fig. 19. Microspore tetrad stage. Only three of the four young microspores are shown. × 600.

two daughter nuclei in various stages of completeness are evident, the spindle fibres still persisting. This phase is of very short duration, and is followed without interval by division of the daughter nuclei, so that the simultaneous production of the four nuclei of the tetrad is effected (Text-fig. 18). The fibres indicating the existence of the spindle between such nuclei are quite evident, and the view shown in Text-fig. 18 is taken from another part of the same microsporangium as that portrayed in Text-fig. 17. This again testifies to the extreme rapidity of the development of the contents of a microsporangium. The fibres soon disappear, each nucleus is invested by its share of cytoplasm, and a wall forms round each young cell, and thus the pollen tetrad still enclosed in the common wall of the mother cell, is evolved (Text-fig. 19). Eventually the pollen grains are set free by the dissolving of the enclosing wall. The tetrads are produced while the flower-bud is at the relatively early stage of development shown in Text-fig. 4. Thereafter the nucleus of each microspore divides (Text-fig. 21, A) and the binucleate condition of the pollen grain is realized (Text-fig. 21, B). Soon after, but in many cases before the opening of the flower bud, four equidistant protuberances are seen to have arisen from the wall of the microspore, thus imparting the characteristic tetrahedral shape of the mature pollen grain (Text-fig. 21, C).



Text-fig. 20. Transverse section of one anther and part of another at the stage immediately preceding dehiscence. *e.*, epidermis; *f.*, fibrous layer; *m.*, binucleate microspores; *t.*, remains of tapetum; *d.*, unthickened cells of fibrous layer indicating region of dehiscence; *c.*, connate cells belonging to two adjacent anthers. × 110.

During microsporogenesis well marked changes fail to be recorded in the development of the tapetum, and wall of the sporangium. As the stamen approaches maturity the cells of the inner layer of the wall—which is only two cells thick—increase in size, and become possessed of a well-marked fibrous thickening (Text-fig. 20). The cells of the outer or epidermal layer, however, shrink, especially those on the side of the microsporangium adjoining the style, and when the time for dehiscence arrives, these epidermal cells have almost collapsed and form no significant part of the mature structure. The fibrous layer completely surrounds the microspores except at the line of dehiscence, and is two cells thick in the region adjacent to the connective. An examination of the fibrous layer reveals the *modus operandi* of dehiscence. The partition wall separating the pairs of microsporangia has already been ruptured, resulting in the formation of two pollen sacs in each anther. The tapetal cells have meantime been absorbed,

their substance being used in the nourishment of the developing pollen grains, and only remnants of the tapetum are now visible. In transverse section the fibrous layer is seen to be complete except in the region *d.*, where two impinging cells (one from each microsporangium of the pollen sac) remain unthickened. Thus a region of weakness extends the whole length of the sac, and when dessication occurs in the mature sacs a strain is set up in the wall, which lends itself to ready dehiscence. It will be obvious that were dehiscence to occur while the anthers still overtop the apex of the style, the microspores shed must drop into the hollow of the indusium. But at this stage, the elongating style begins to push the cup-shaped indusium up through the narrow passage between the connate anthers, and in no case have pollen grains been found in this cup prior to its passage up through these anthers. Accordingly, the friction set up by the indusium rubbing against these anthers is the stimulus which determines the actual time of dehiscence. It is worthy of note that this rapid elongation of the style terminates in the opening of the bud, and at the time when the microspores have just reached the binucleate condition. The full significance of this exact mechanism for abstracting the contents of the pollen sac, and the placing of the pollen grains in a position favouring dispersal by visiting insects, will be appreciated later when the problem of pollination is under discussion.

The Male Gametophyte.

The flower of *Dampiera stricta* is markedly protandrous, and the uninucleate microspores are produced in the young flower bud (Text-fig. 5). Soon after, and before the flower opens the nucleus undergoes division (Text-fig. 21, A) and the

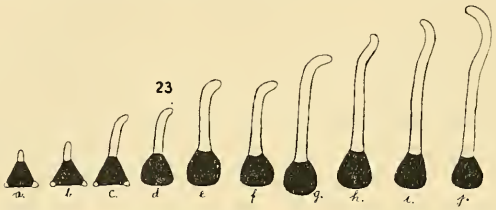
Text-fig. 21. Three consecutive stages in development of male gametophyte. × 600. A. Nucleus of microspore dividing. B. Binucleate stage. *v.*, vegetative nucleus; *g.*, generative nucleus. *C.* Tetrahedral condition of mature microspore with slight protrusion of intine at three of the four corners.

Text-fig. 22. Two microspores *m.* and m_1, with pollen tubes *p.* and p_1, passing down among receptive papillate cells of stigma. × 266.

binucleate stage is reached (Text-fig. 21, B). Meanwhile the outer wall of the spore is steadily increasing in thickness until a relatively thick exine is produced. This thickening is not uniform, however, and in the mature pollen grain four thin areas are discernible (Text-figs. 21, B, and 21, C). By the time the flower bud opens the pressure of the protoplasm within the pollen grain has in many cases increased to such a degree that four distinct protuberances are produced by the protrusion of the spore wall at the four unthickened regions. This gives the microspore the tetrahedral shape characteristic of the mature pollen grain.

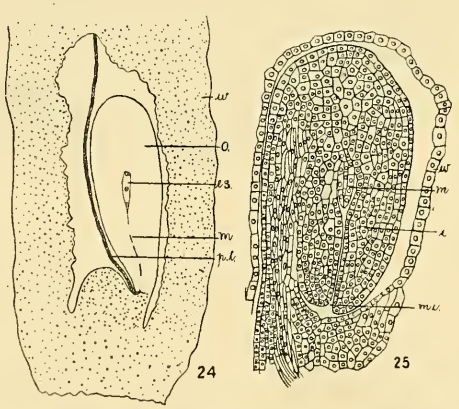
In order to study the further development of the male gametophyte a number of mature microspores were removed from the flower and placed in a five per cent.

solution of cane sugar contained in a well-slide. This preparation was then placed under the objective of a microscope. After half an hour one of the four protuberances in each of several microspores under observation was seen to have increased in size as shown in Text-fig 23, *a*. Thereafter the young pollen tube steadily increased in length, and its appearance at intervals of fifteen minutes was noted and drawn (Plate xxxvii, fig. 6). Thus was obtained the series of



Text-fig. 23. Series showing development of pollen tube in a five per cent. sugar solution. × 225 (approx.).

drawings indicated in Text-fig. 21, *a.-j.* The last drawing of the series, 21 *j.*, accordingly represents the development attained in 2 hours 45 minutes. It will be observed that the other three protuberances steadily contract as germination proceeds, and eventually disappear. The pollen tube therefore develops with great rapidity, and several such tubes may be detected when a mature style is teased out under the microscope.



Text-fig. 24. Pollen tube within ovary, and passing from style to micropyle. *w.*, wall of ovary; *o.*, ovule; *m.*, micropyle; *p.t.*, pollen tube; *e.s.*, embryo sac. × 16.

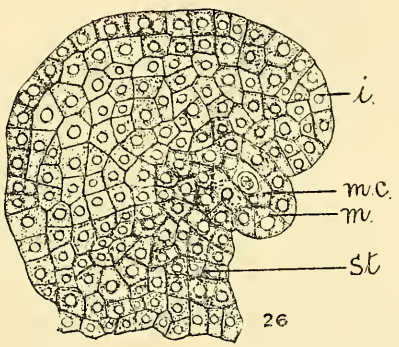
Text-fig. 25. Median longitudinal section of ovary showing anatropous nature of young ovule. *i.*, single massive integument; *m.i.*, micropyle; *m.*, megasporangium; *w.*, wall of ovary. × 66.

Further development was traced by examining longitudinal sections of the ovary. In Text-fig. 24, a pollen tube is seen passing from the base of the style to the micropyle of the ovule. In this case only a single pollen tube is shown, but in nearly every case examined several pollen tubes were in evidence. These either grew along the surface of the ovule or adhered to the inner wall of the

ovary until the region of the micropyle was reached. One of the pollen tubes eventually makes its way through the micropyle and enters the embryo sac in the region of the egg-apparatus.

The Megasporangium.

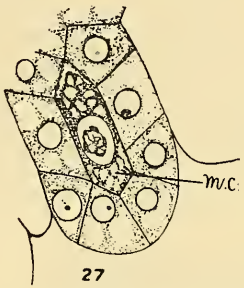
The gynoecium is composed of two carpels, the origin and early development of which have already been referred to. The young carpels arise separately, but as growth proceeds fusion occurs, and a common style, stigma, and ovary arise. Growth at the apex of the thalamus is, however, relatively slow, and so the carpel producing region is gradually overtopped by the stronger growth around it. The ovary thus becomes inferior, but the style and stigma protrude above the encircling thalamus. The cavity of the ovary is shown in Text-fig. 3, with a young nucellus arising therein. So far there is no indication of an integument. A slightly older stage is shown in Text-fig. 4. Even at this early stage the anatropous nature of the mature ovule is foreshadowed. A single massive integument has



Text-fig. 26. Median longitudinal section of very young ovule. The thick integument partially enclosing the megasporangium is seen. *i.*, integument; *m.*, megasporangium; *m.c.*, megaspore mother cell; *st.*, funiculus. × 266.

made its appearance, and partly encloses the nucellus which forms a relatively small portion of the ovule. Text-fig. 26 illustrates the structure of the very young ovule, at a stage slightly younger than that just referred to. The funiculus, integument and megasporangium are apparent, the last named consisting of an axial row of cells surrounded by a jacket one-cell thick. The megasporangium is therefore of the reduced type characteristic of the more highly developed Angiosperm families. As development proceeds the integument soon outstrips the nucellus, which becomes completely enclosed except for the micropylar passage at the distal end. Various stages of this envelopment are illustrated in Text-figs. 4, 5, 6, 7, 25, 26 and 29. The long micropyle leading from the apex of the nucellus is shown in Text-figs. 25 and 29. It is to be noted that thus early the cells of the integument bordering on that region of the micropyle adjacent to the megasporangium are densely cytoplasmic, and clearly in a state of high nutrition (Text-fig. 29). Later on, the functional megaspore and embryo sac grow forward into the micropyle, and eventually attain a position just beyond this nutritive jacket, which functions as a tapetum, a feature not uncommon in representatives of the more highly developed Angiosperms.

In dealing with this structure Coulter and Chamberlain (1915) point out that it is usually derived from the integument, but arises from the nucellus in *Armeria*. They observe: "This jacket has been definitely observed as conspicuous in *Helosis* (Chodat and Bernard, 1900), *Sium*, many Scrophulariaceae (Balicka-Iwanowska, 1899), *Campanula* (Barnes, 1885), Stylidaceae (Burns, 1900) and certain



Text-fig. 27. Median longitudinal section of megasporangium. The large cell terminating the axial row of the megasporangium is the megaspore mother cell, *m.c.*. × 450.

Compositae, and by Billings (1901) in numerous Sympetalous forms, among the most conspicuous being *Lobelia*. Primulaceae (except *Leptosiphon*), *Linum*, *Forsythia*, *Amsonia*, *Menyanthes*, Polemoniaceae, *Myoporum*, *Globularia*, *Scaevola*, *Calendula*, etc.".

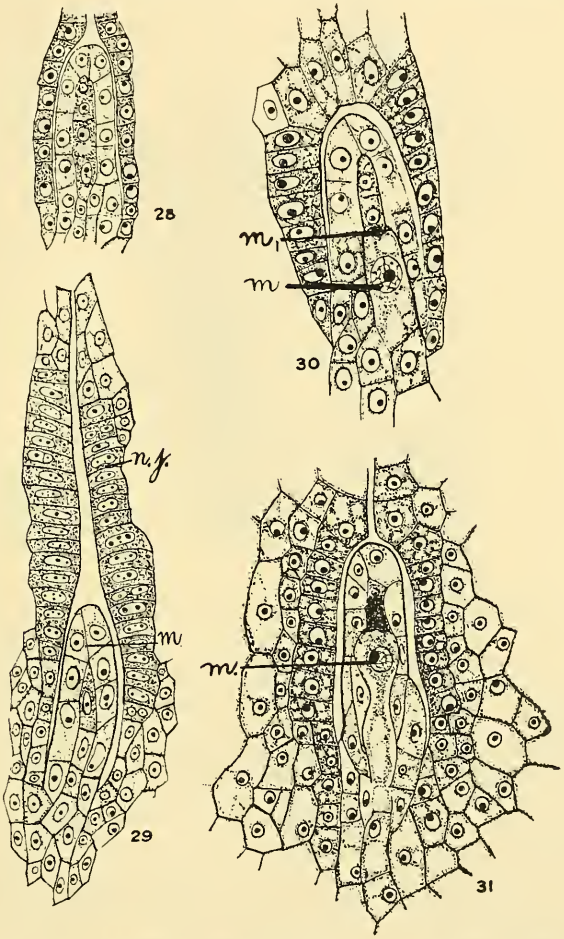
From this list it is evident that a nutritive jacket around the embryo sac is of frequent occurrence among the Sympetalae (especially amongst the more highly developed families) but is also known amongst the Archichlamydeae though to a much less extent.

Just when the anatropous nature of the ovule has become apparent, it is seen that the distal cell of the axial row of the nucellus is large relative to the others, and has a nucleus in proportion. This cell is clearly a megaspore mother cell, and it continues to enlarge until of the dimensions shown in Text-figs. 26 and 27. The nucleus is in synapsis, but examination of numerous longitudinal sections of buds about this stage of development, failed to demonstrate actual reduction division. However, a subsequent stage is indicated in Text-fig. 28 where the four nuclei of the megaspore tetrad are visible. These are not separated by cell walls. A further stage in development is shown in Text-fig. 30 where the two nuclei towards the distal end are quite evident, but the third is undergoing disintegration. The reason for this is seen when the fourth, innermost, or chalazal nucleus is examined. It easily exceeds all the others in dimensions and is clearly the functioning megaspore. Its growth has resulted in the partial disintegration of the adjacent nucleus which is seen in a matrix of deeply stained matter. The steady increase in size of the functional megaspore results in the disorganization of the other three megaspores as illustrated in Text-fig. 31, where only a remnant of the distal nucleus is discernible, the other two non-functional megaspores having completely disappeared. Their former position is occupied by a dark coloured mass which stains very deeply with Haidenhain's iron alum and Fleming's triple stains respectively. Eventually this mass—which evidently is used in the

nutrition of the functional megaspore—completely disappears, and the young embryo sac with its large nucleus is evolved (Text-fig. 32).

The Female Gametophyte.

Meanwhile the nutritive jacket is becoming more and more evident, extending well down the micropyle, and also completely surrounding the megasporangium.



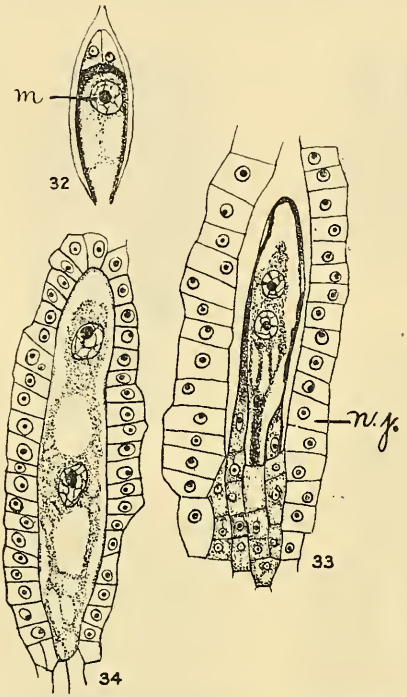
Text-fig. 28. Median longitudinal section of slightly older ovule showing 4 megaspores not separated by walls. × 266.

Text-fig. 29. Longitudinal section through micropyle showing nutritive jacket, *n.j.*, formed by innermost cells of integument. The megasporangium, *m.*, is not quite in median section. × 266.

Text-fig. 30. Median longitudinal section of megasporangium showing enlarged functional megaspore, *m.*, and the adjoining megaspore, $m._1$, disintegrating. × 333.

Text-fig. 31. Median longitudinal section of megasporangium showing functional megaspore, *m.* The disintegration of the other three megaspores is almost complete. × 333.

As the functional megaspore increases in size, the single layer of cells forming the wall of the megasporangium is steadily encroached upon and absorbed (Text-fig. 32), so that by the time the young embryo sac has been formed, the wall cells have practically disappeared. The nucleus of the surviving megaspore now divides, producing the first two nuclei of the female gametophyte (Text-fig. 33).



Text-fig. 32. Longitudinal section of ovule showing functional megaspore, *m*., and remains of nucellar tissue now almost absorbed by developing embryo sac. × 300.

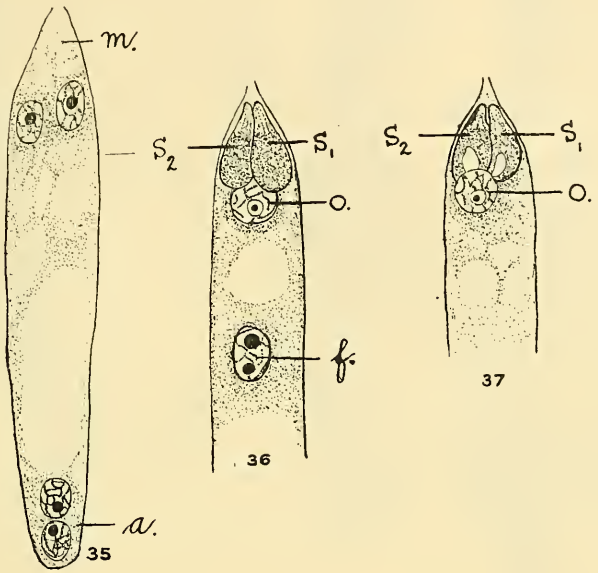
Text-fig. 33. Portion of median longitudinal section of an ovule showing binucleate condition of embryo sac. *n.j.*, nutritive jacket. × 300.

Text-fig. 34. Binucleate condition of embryo sac slightly older than that figured in previous drawing. × 310.

The embryo sac and nuclei enlarge rapidly, the latter being gradually separated (Text-fig. 34), and eventually occupying opposite ends of the sac. Each nucleus divides again producing the four-nucleate stage illustrated in Text-fig. 35. A subsequent division of each of these nuclei results in the eight-nucleate stage of the mature gametophyte. Text-figs. 36 and 37 respectively show the micropylar portions of the two embryo sacs. In each case the egg apparatus is depicted, while in the former the endosperm nucleus is represented.

Text-fig. 38 shows three successive sections of a mature and enlarged embryo sac. In B a single synergid and the egg are apparent; in A a second synergid and the micropylar polar nucleus are evident; while in C the antipodal polar nucleus and the three antipodal cells are found. The synergids are pyriform, their

tapering ends invade the micropyle to some slight extent, and each possesses a nucleus and a large vacuole. The oosphere is apparent at the lower extremities of the synergids. The tapetum is figured on one side of the embryo sac only. This nutritive jacket is now at the height of its development, and its dense deeply



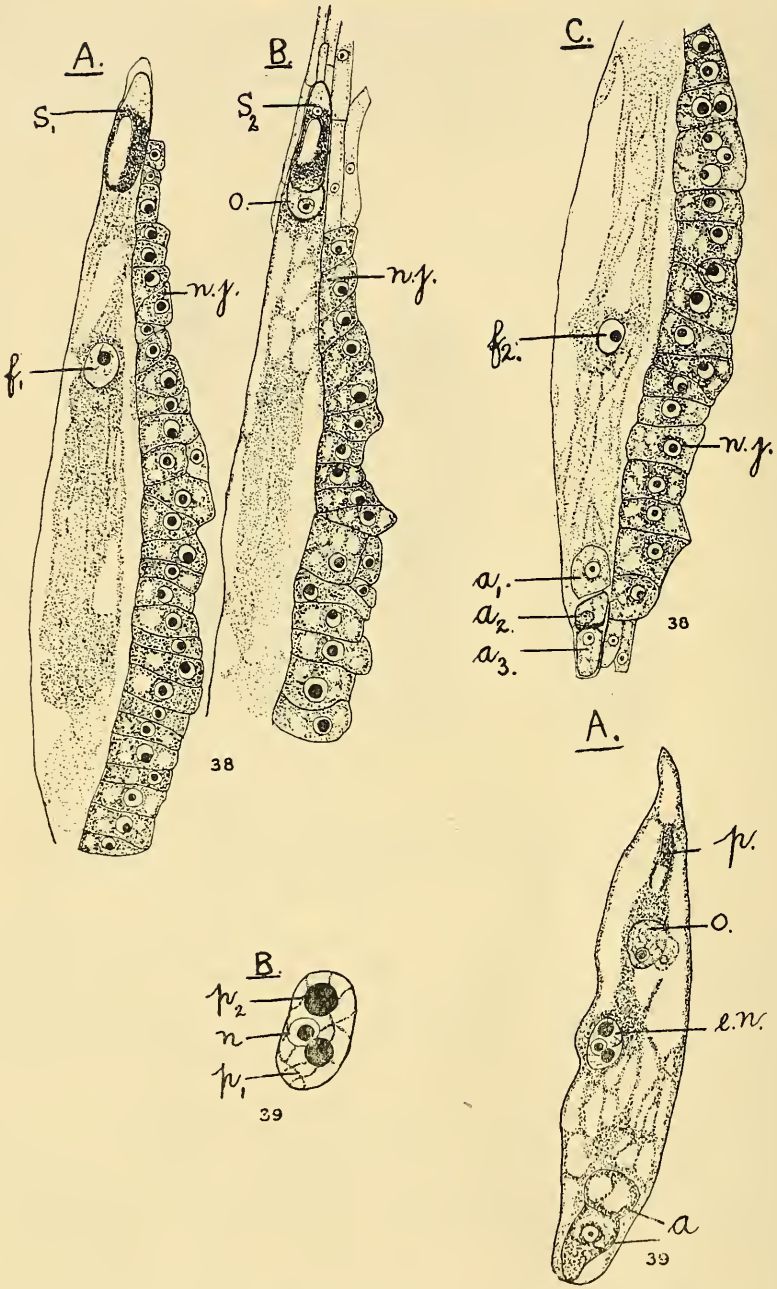
Text-fig. 35. The four-nucleate condition of the embryo sac. *m.*, micropylar region of sac; *a.*, antipodal region of sac. × 266.

Text-figs. 36 and 37. Micropylar region of two embryo sacs. $s._1$ $s._2$, synergids; *o.*, oosphere; *f.*, primary endosperm nucleus. × 266.

stained cytoplasm, coupled with the regular arrangement of its constituent cells brings it out in bold relief in the sections. It will be seen that the micropylar region of the sac has grown slightly beyond the tapetal cells of this region. A slightly older stage of the sac is seen in Text-fig. 39, A. Therein the egg, the fusing polar nuclei, and two of the antipodal cells are delineated. Part of the pollen tube is visible, and what are interpreted as the two male nuclei—one in contact with the egg and another with the fusing polar nuclei—are indicated.

It must be admitted, however, that these preparations were not distinct enough to diagnose the male nuclei with absolute certainty nor to place the behaviour of the male nuclei beyond the possibility of doubt. The view of what is regarded as the triple fusion nucleus, as obtained under the oil-immersion lens, is shown in Text-fig. 38, B.

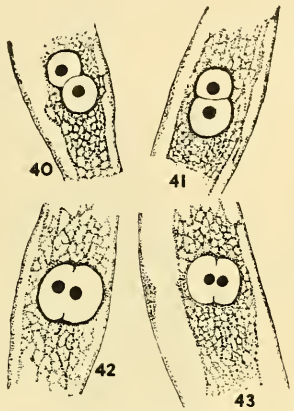
The behaviour of the polar nuclei, however, presented no difficulties, as their history could be traced with considerable ease. Their gradual fusion is illustrated in Text-figs. 40-43, but in none of the cases illustrated is the second male nucleus in evidence.



Text-fig. 38. Text-figs. 38A, 38B and 38C show views seen in three successive sections of embryo sac. $s._1$, synergid; $s._2$, synergid; *o.*, oosphere; $f._1$, micropylar fusion nucleus; $f._2$, antipodal fusion nucleus; $a._1$, $a._2$ and $a._3$, antipodal cells; *n.j.*, nutritive jacket shown on one side of embryo sac only. × 266.

Text-fig. 39. A. Another embryo sac. *o.*, oosphere; *e.n.*, endosperm nucleus; *a.*, antipodal cells; *p.*, pollen tube. × 266. B. Fusion of polar nuclei, $p._1$ and $p._2$, with male nucleus, *n.* × 600.

The chalazal region of the embryo sac is occupied by three antipodal cells. These are well developed and vary in shape and size, the one occupying the lower extremity of the sac being somewhat elongated, while the other two are almost



Text-figs. 40-43. Polar nuclei in various stages of fusion. × 300.

isodiametric. These cells remain active until after fertilization, evidently functioning in passing nourishment from the chalaza of the ovule into the developing sac, but unlike the antipodals found in many of the higher Sympetalae, *e.g. Aster novae-anglicae* (Chamberlain, J. C., 1895), *Sherardia arvensis* (Lloyd, F. E., 1902), do not become unduly enlarged, nor do they encroach to any extent on the chalazal region as haustorial invaders.

The endosperm nucleus divides before that of the fertilized egg or oospore giving rise to free endosperm nuclei as demonstrated in Text-fig. 44. The embryo sac is long and narrow at this stage, so that comparatively few free endosperm nuclei are formed before wall formation is initiated. This is accompanied by rapid expansion of the sac. The nutritive jacket still persists unimpaired.

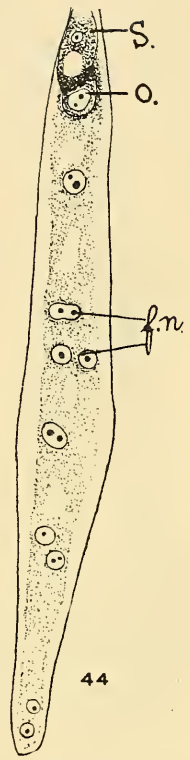
Embryogeny.

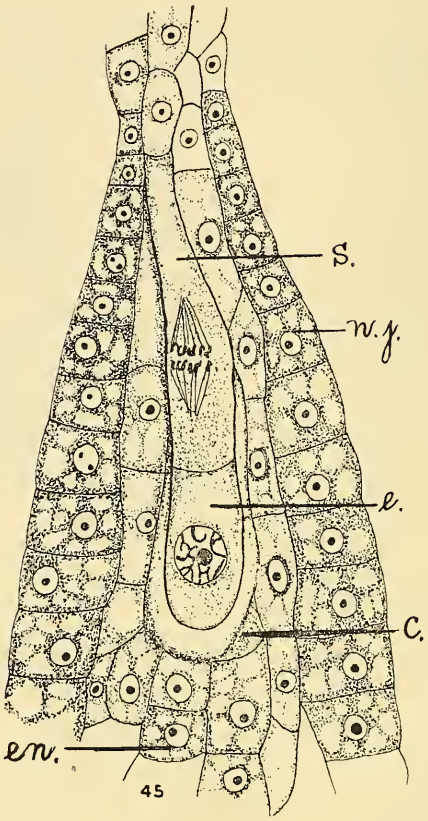
When the oospore divides and commences to produce the embryo, a large mass of endosperm tissue awaits invasion. The details of embryogeny are illustrated in a series of drawings (Text-figs. 45-52).

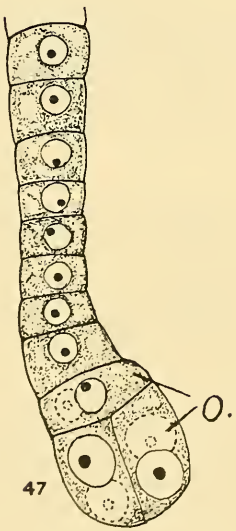
Actual division of the oospore has not been demonstrated, but Text-fig. 45 shows the stage immediately subsequent. Examination reveals a pro-embryo of two cells—a basal or embryo cell proper, and a suspensor cell. The nucleus of the latter is in mitosis.

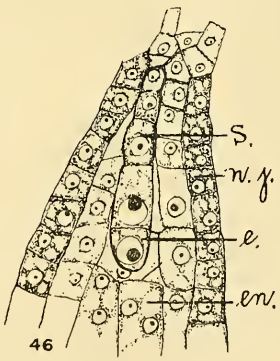
The pro-embryo invades the endosperm tissue, the cells of which are being absorbed. The cells of the young embryo evidently secrete an enzyme which gradually brings the contingent endosperm cells into solution, preparatory to absorption. The digestive action of the embryo is indicated by the corroded appearance of the adjacent endosperm cells. This feature is apparent in Text-figs. 45, 48 and 51.

The cells of the nutritive jacket still preserve their form, but are now distinctly vacuolate. Text-figs. 45, 46 and 48 show the gradual production of the suspensor which pushes the embryo cell well down amid the endosperm cells.







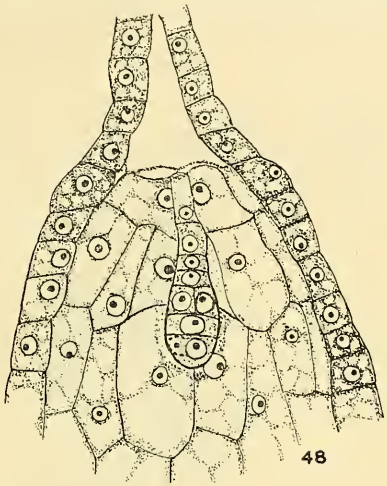


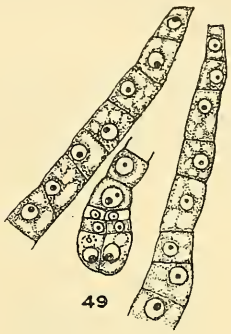
Text-fig. 44. A longitudinal section through an embryo sac after fertilization. *s.*, synergid; *o.*, oospore; *f.n.*, free endosperm nuclei. × 266.

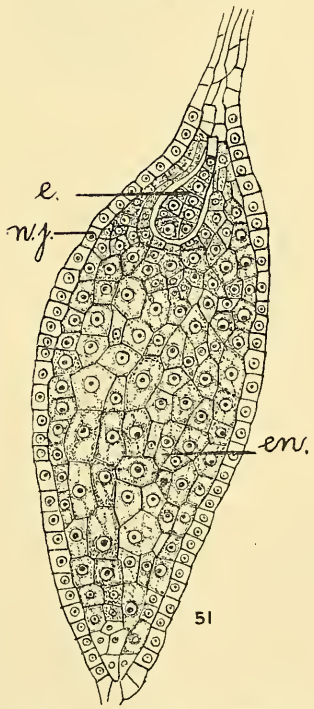
Text-fig. 45. Very early stage in embryology soon after division of oospore. *e.*, embryonal cell; *s.*, first cell of suspensor with nucleus undergoing division; *n.j.*, nutritive jacket; *c.*, corroded cells of endosperm tissue. × 600.

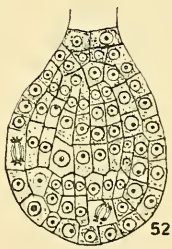
Text-fig. 46. A slightly older stage of embryo. The suspensor has elongated. *e.*, embryonal cell; *s.*, suspensor; *en.*, endosperm; *n.j.*, nutritive jacket. × 266.

Text-fig. 47. A further stage in development of embryo. The embryonal cell has divided and approached the octant stage, *o.* × 600.









Text-figs. 48-50 show further stages in embryogeny. × 266.

Text-fig. 51. Embryo, *e.*, invading the endosperm, *en.*; *n.j.*, nutritive jacket around sac. × 150.

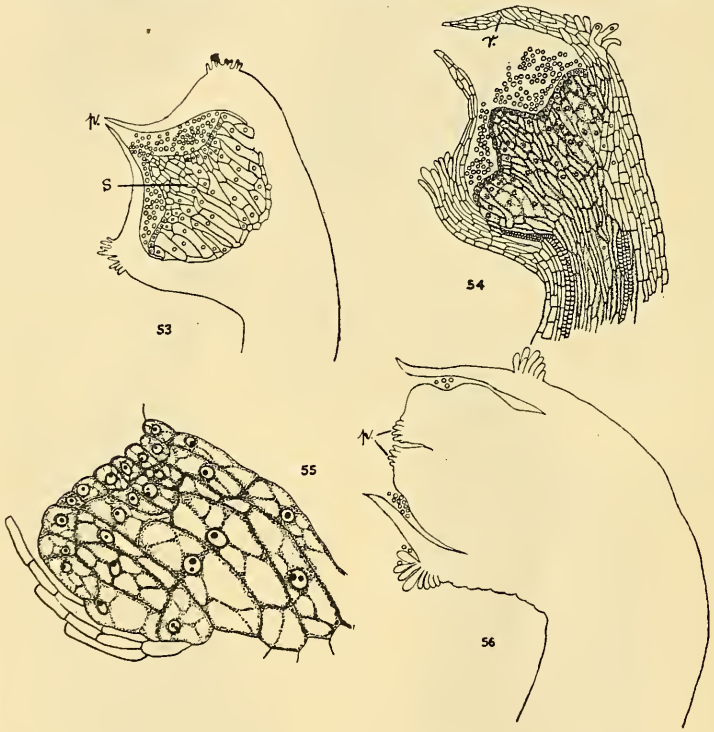
Text-fig. 52. Late stage in embryogeny. The dermatogen, periblem and plerome are differentiated. × 266.

Finally the terminal cell divides so that the quadrant stage, and later the octant stage, are arrived at (Text-fig. 47).

Further cell division follows the octant stage, as indicated in Text-figs. 49-52, and eventually the relatively mature condition depicted in Text-fig. 52 is arrived at. Therein the dermatogen is well defined, and the differentiation into periblem and plerome suggested. Beyond this stage the development of the embryo was not traced.

Pollination.

The problem of pollination and the mechanisms incidental thereto in the Goodeniaceae have attracted widespread attention. Several investigators—notably Brown, R. (1818, 1866), Mueller, H. (1883), Haviland, E. (1884, 1885), Haviland, F. E. (1914), and Hamilton, A. G. (1885, 1894), have placed the results of their



Text-fig. 53. Longitudinal section of apex of style. The young stigma, *s.*, is growing up from the base of the pollen cup, and forcing out the microspores through the apical pore, *p.* × 73.

Text-fig. 54. Another view of same showing conducting tissue of style. The portion of the cup *r.* has been slightly displaced in cutting the section. × 73.

Text-fig. 55. Part of stigma of previous figure shown under a higher power of magnification in order to illustrate nature of component cells. × 133.

Text-fig. 56. Longitudinal section of an older stage of style showing stigma occupying centre of pollen cup. The bi-lobed nature of stigma, and the central papillate cells, *p.*, are evident. × 33.

investigations on record in the case of certain species of *Goodenia*. The conclusions arrived at are so varied, however, that a careful study of the method of pollination in other genera of the family seems advisable.

In the case of *Dampiera stricta* the method of dehiscence of the anthers, and the depositing of the pollen grains within the hollow indusium have already been described. The cup is filled to overflowing, the spores forming a pyramidal mass. Thereafter the indusium closes owing to the contraction of the margins.

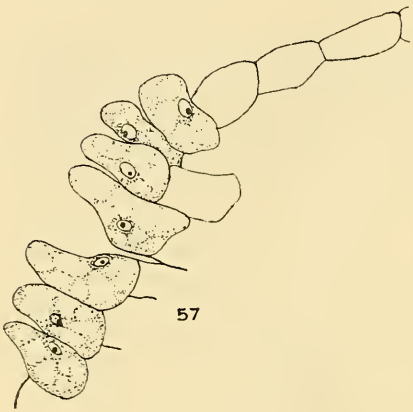
At the time when the style finally elongates, and the flower bud is on the point of opening, the indusium is forcibly thrust into a chamber formed by the auricles in the line of junction between the two posterior petals. The two flap-like appendages aid in the complete enclosing of the indusium, which is orientated so as to face the anterior side of the flower. At no period then, has the pollen been exposed, although part of the bent style is visible, outside the corolla between the two posterior petals. By this time the anthers have withered, and are of no further significance. The rudimentary stigma at the base of the closed indusium now commences to grow rapidly (Text-figs. 53 and 54) and gradually pushes the pollen in front of it, and out through the narrow aperture now present at the top of the fringed pollen cup (Plate xxxvii, figs. 3, 4 and 5). The pollen thus ejected either lodges on the outer sloping sides of the indusium, as indicated in the photographs just referred to, or is deposited in the chamber in which the indusium is imprisoned. Obviously such pollen grains cannot regain their former position resting on the apex of the stigma. Eventually the steadily expanding and rounded stigma protrudes above the rim of the inner cup of the indusium (Text-fig. 56) and occupies the cavity formerly filled by pollen grains. A few microspores may remain lodged between the lower portion of the stigma and the inner wall of the indusium, but such are ineffective from the point of view of pollination. The stigma finally becomes slightly two-lobed, and the cells within and around the depression so formed become papillate, and eventually receptive in relation to the pollen grains (Text-figs. 56, 57 and 22). Furthermore, the sub-epidermal cells immediately within this cleft, and also the tissue leading therefrom, and down through the centre of the style are of a loose, thin-walled nature. Such cells have all the characters of a typical conducting tissue for the nutrition of the advancing pollen tube. Pollen tubes in considerable number were found when the central tissue of the style was dissected out, and examined under a microscope.

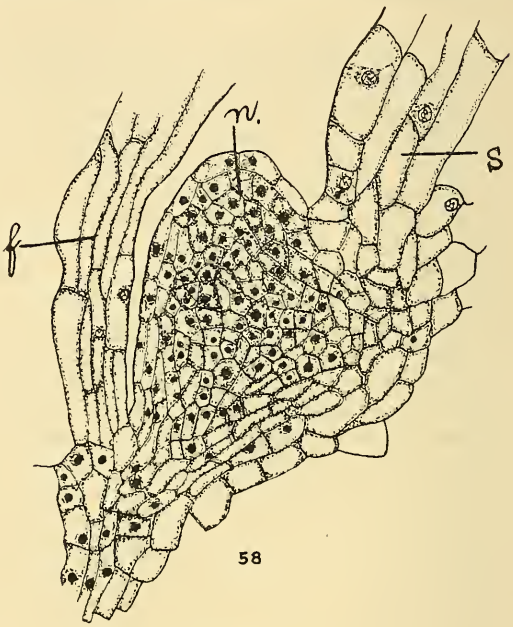
In no case were microspores seen to germinate while still within the indusium, although at this stage they are in the binucleate condition, and in many cases show the slight protrusion of the intine through the four weak areas in the exine characteristic of the mature microspore. Judging from the various stigmas examined, at different stages of growth up to and including the emergence of the stigma from the indusium, it seems clear that the pollen grains do not germinate within their own indusium.

Evidently, then, the stigma does not become receptive until the pollen grains from the same flower have been ejected from the pollen cup.

Now, five well developed nectaries are found at the base of and within the whorl of stamens. These are obviously related to insect visitation, and it is well known that bees are frequent visitors to the flower in question. That insects are instrumental in the transference of pollen is proved by the fact that in one case foreign pollen was actually found on a stigma examined. The contrast which this pollen (which was round and spiny) made with the characteristic microspores of *Dampiera*, rendered this point peculiarly easy of elucidation. The foreign

pollen had not germinated. From what has already been demonstrated in regard to the rate of growth of the pollen-tube (Text-fig. 23), it follows that fertilization may occur within a few hours of the pollen being deposited on the ripe stigma. An insect entering the flower pushes the two adaxial perianth segments apart, and, at the same time releases the pollen cup from its chamber. Pollen thus falls on the visitor, and such action will continue until all the pollen has been removed,





Text-fig. 57. Papillate cells of stigma under higher power of magnification. × 266.

Text-fig. 58. Longitudinal section of nectary, *n.*, situated at base of style, *s.*, and within filament of stamen, *f.* × 150.

a consummation which may well be effected before the stigma becomes receptive. Pollen from the pouch is also removed at this stage. It was also observed that a considerable proportion (about 20% or more) of the pollen grains never reach maturity. Thus when the stigma becomes receptive the pollen grains have either been removed by insects or have been pushed aside, and so subsequent insects will deposit pollen from their backs or heads on the surface of the receptive stigma.

It must be conceded then, that pollen is actually transferred by insects from one flower of *Dampiera stricta* to another flower on the same or on another plant, and so cross pollination is effected.

It is not impossible, however, that self pollination may occur in the event of the flower not being visited by the insects, although the writer is of the opinion that the available evidence is against the view that self-fertilization does actually occur. The point can be settled only by taking means to prevent the access of foreign pollen, and then determining whether embryos have formed in the ovaries concerned. The writer hopes to elucidate this point in the near future.

An experiment of this nature has already been carried out in the case of

Goodenia cycloptera by Haviland, F. E. (1914), who found that embryos were not formed.

A survey of the facts laid bare by this investigation of various phases in the life-history of *Dampiera stricta* reveals few features differing markedly from those characteristic of the various forms comprising the higher Sympetalae. The details of organogeny, microsporogenesis, megasporogenesis and embryogeny conform to type, and indicate that the Goodeniaceae find their natural position in the order Campanales. The genus *Dampiera* despite its being endemic to Australia does not show any signal aberrant features, such as was laid bare by an examination of another great Australian family, namely the Epacridaceae, a member of which, *Styphelia longifolia* (Brough, 1923, 1924), showed unique characters more especially in megasporogenesis.

Reverting to *Dampiera* it is interesting to observe the syngenesious anthers—a feature so characteristic of the Campanales. The piston-like action of the style is also typical, but *Dampiera* with its protandry, pollen cup, delicate anther dehiscence, method of dispersing the pollen, and the very late exposure of receptive stigmatic cells is perhaps the most outstanding in an Order noted for its highly developed pollinating mechanisms. The genus would seem to present an epitome of the many peculiarities portrayed by the various members of the most recent and specialized of all the Orders of flowering plants.

On looking for genetic relationships between the Goodeniaceae and the other members of the Order Campanales certain striking features already noted in *Dampiera* are seen to be reflected in the tribe Lobelioideae of the Campanulaceae. In this tribe one finds the herbaceous habit, the zygomorphic flowers, the blue corolla often split to the base, the syngenesious anthers, the piston-action of the style, and the nutritive jacket around the embryo sac. The genus *Lobelia* is represented by eighteen species in Australia (Bentham and Hooker), and the writer has come to the conclusion that all the available evidence goes to show that the genus *Dampiera*—if not the Goodeniaceae as a whole—has been derived from the Lobelioideae.

Summary.

Organogeny. The primordia of the various sets of floral organs arise separately and in acropetal succession. The five young sepals eventually fuse, and form a gamosepalous calyx joined to the ovary. The five petal primordia maintain their identity until an advanced stage of bud development has been attained, when the three abaxial segments fuse to form the lower lip, while the two remaining adaxial segments form the upper lip which is split almost to the base. The two lips are separate throughout. The stamens retain their identity until about the microspore mother cell stage, when the syngenesious condition arises by fusion of contiguous cuticles of the anthers.

The two young carpels fuse to form a common style and inferior ovary.

The characteristic pollen cup arises during late bud development by the relatively slow rate of growth at the organic apex of the style, and the increased merismatic activity in the marginal region.

Microsporangium. The archesporial cells divide by periclinal walls giving rise to a primary parietal layer and a primary sporogenous layer. The cells of the former divide once thereby producing a wall layer and the tapetum. The cells of the primary sporogenous layer divide two or three times before attaining the spore mother cell stage.

The spore mother cells undergo reduction division and then ordinary somatic division, whereby simultaneous pollen tetrads are produced. The great rapidity in growth is attested by the wide range in development depicted in the longitudinal section of a single sporangium. In the mature pollen sac the spores are binucleate, each spore wall bears four equidistant thin areas, the hypodermal cells constitute the fibrous layer, and dehiscence is effected by longitudinal splitting along two median vertical contingent rows of unthickened cells of the hypodermal layer. The mature stamens are short, and are never exposed outside the flower.

The male gametophyte. The mature tetrahedral pollen grain contains a generative and a vegetative nucleus. During germination a single pollen tube grows out through one of the four unthickened areas of the mature microspore. Evidence testifying to the rapidity in growth of the pollen tube was obtained by careful observation of its development in a five per cent. sugar solution. Pollen tubes were traced from the receptive cells of the stigma, throughout the style, and in the ovary from the base of the style to the micropyle. The tube grows through the micropyle, and enters the embryo sac in the region of the egg apparatus.

The megasporangium. A solitary nucellus arises within the ovary. A single thick integument gradually encloses the young megasporangium, which consists of an axial row of cells surrounded by a jacket one cell thick. The anatropous nature of the ovule is early foreshadowed. The megaspore mother cell is formed at the micropylar end of the axial row of the megasporangium. The mother cell gives rise to a linear tetrad of megaspores, the innermost of which is the functional megaspore; this develops rapidly and absorbs the other three megaspores. The wall cells of the megasporangium are also absorbed. Meantime the cells of the integument lining the micropyle enlarge, become densely cytoplasmic, and eventually form a very definite and noteworthy nutritive jacket around the embryo sac.

The female gametophyte. The functional megaspore increases in size, and steadily invades the micropyle. During this development, the bi-nucleate, four-nucleate, and eight-nucleate stages of the female gametophyte are attained. The egg apparatus, polar nuclei, and antipodal cells are normal in structure and polarity. These are described in detail.

Fertilization. The pollen tube enters the embryo sac. One male nucleus fertilizes the oosphere, while the other joins the partially fused polar nuclei.

Endosperm formation. The endosperm nucleus divides before that of the oospore—free endosperm nuclei being formed. Wall formation, accompanied by rapid growth of the embryo sac then supervenes. A massive endosperm is formed.

Embryogeny. The oospore commences development soon after wall formation in the endosperm has been initiated. A long suspensor is formed which pushes the terminal cell well down into the soft endosperm tissue. The embryonal cell attains the quadrant and octant stages respectively. Later periclinal walls cut off the dermatogen, and in the final stages examined, the periblem and plerome had been differentiated.

Pollination. Many investigators, for example R. Brown, H. Mueller, E. Haviland, F. E. Haviland, and A. G. Hamilton, have carried out investigations regarding the methods of pollination in members of the Goodeniaceae. Conflicting views have been expressed. In the case of *Dampiera stricta* the elongating style carries the pollen cup up through the syngenesious mature anthers causing

introrse dehiscence of the microsporangia, and the filling of the cup with pollen grains. The style further elongates and thrusts the cup into a pouch in the line of junction of the two adaxial segments of the corolla. The cup is orientated so as to face the centre of the corolla. The stigma then arises from the base of the pollen cup, and very gradually forces the microspores out through the pore at the apex. Such microspores are then in a suitable position for removal on the backs of visiting insects. Eventually the fully developed and slightly bi-lobed stigma occupies the whole of the interior of the cup. Then, and not till then, do receptive cells appear in the apical region of the stigma, which is now ready to receive pollen from insect visitors coming from less mature flowers.

A very exact mechanism to ensure cross pollination is thus demonstrated. It would seem, however, that self pollination is possible in the absence of insect visitors.

The evidence derived from this investigation strongly supports the view that the genus *Dampiera* is derived from the Lobelioideae.

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EXPLANATION OF PLATES XXXVI-XXXVII.

Plate xxxvi.

1. General habit of *Dampiera stricta*; about one-third natural size
2. Flowers of *D. stricta*; about one and a half times natural size.

Plate xxxvii.

3. Style supporting pollen cup with narrow orifice through which microspores are being gradually ejected.
4. A style slightly more advanced than that of previous figure. The pollen cup is now at right angles to main style. The gradual ejection of microspores from the pollen cup is illustrated.
5. View showing the short stamens arranged around the style. The anthers have separated, and dehiscence has occurred.
6. Microspores germinating. × 100 (approx.).